

OBSERVATIONS AND EXPERIMENTS ON THE PHYSIOLOGY OF MEDUSAE

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Since the classical work of Romanes (1885) and the experiments of Morse (1906, 1907), Murbach (1903, 1907, 1909), Yerkes (1902, 1904, 1906), and Yerkes and Ayer (1903) on *Gonionemus*, there have been very few studies of the behavior and other general aspects of the physiology of hydroid medusae. Gemmill (1919) gave an account of the flagellar currents of *Mericertum*, Harvey (1921) studied bioluminescence in several Puget Sound medusae, Weese and Townsend (1921) tested the reactions of *Aequorea* to pH, temperature, and salinity, and Milne (1938) and Edney (1939) have published some notes on the behavior of fresh-water medusae. During a stay at the Oceanographic Laboratory, Friday Harbor, Washington, in the summer of 1938, I was led by the great abundance of hydromedusae in those waters to make some observations upon several matters. My principal object was to study the course of food in the gastrovascular system, a matter on which, so far as I am aware, no exact knowledge was available. Some other points were also investigated.

As material, five common Puget Sound medusae were utilized: *Aequorea aequorea*, *Halistaura cellularia*, *Phialidium gregarium*, *Stomatoca atra*, and *Sarsia mirabilis*. These species can be obtained near the dock in front of the laboratory buildings in great abundance at practically any time. Some observations were also made on *Gonionemus vertens* and the stalked scyphozoan *Halicystus sanjuanensis*. The animals were studied immediately after being brought in from the Sound or in many cases were observed directly from the dock.

WATER CONTENT

Recently (1938), I presented some data on the water content of *Aurelia*, and reviewed the available literature. As nearly all the data concern scyphozoan medusae, it seemed desirable to obtain some figures on hydroid medusae. Accordingly, freshly collected specimens of *Aequorea*, *Halistaura*, *Phialidium*, and *Sarsia* were given a quick rinse in fresh water, dried on paper toweling, and weighed to the third place

in previously weighed beakers. They were then dried in an electric oven kept at 100° C., and the drying was completed to constant weight in a desiccator over CaCl₂. *Aequorea* and *Halistaura* are large species and were determined singly. In the case of the small species *Sarsia* and *Phialidium*, a number of specimens were used for each determination, as shown in Table I. The smallest available specimens of *Aequorea* were also determined for comparison with fully grown animals and two

TABLE I

Water content of Puget Sound hydroid medusae, arranged in order of decreasing weight. Salinity of sea water, 3.09 per cent.

Large Aequorea				Halistaura			
No. animals	Wet weight	Dry weight	Percentage water	No. animals	Wet weight	Dry weight	Percentage water
1	34.303	1.182	96.56	1	20.422	0.709	96.53
1	31.594	1.092	96.55	1	20.389	0.709	96.53
1	27.976	0.960	96.57	1	19.091	0.655	96.57
1	24.787	0.843	96.60	1	14.402	0.497	96.55
1	20.963	0.726	96.54	1	13.265	0.457	96.56
Small Aequorea				Sarsia			
2	8.669	0.296	96.59	5	2.350	0.080	96.60
3	12.647	0.387	96.94	6	2.549	0.090	96.47
2	6.395	0.204	96.81	22	8.343	0.269	96.78
3	8.555	0.258	96.99	7	2.459	0.085	96.55
3	8.522	0.273	96.80	18	2.838	0.090	96.83
2	5.667	0.194	96.58	Phialidium			
3	7.101	0.241	96.61				
3	6.346	0.205	96.77				
3	6.136	0.211	96.57				
3	4.589	0.134	97.08				
				12	4.923	0.165	96.65
				13	5.137	0.147	97.14
				18	6.975	0.243	96.52
				20	6.313	0.207	96.71
				15	4.558	0.157	96.56
				18	4.104	0.136	96.69

or three were weighed together in each case. The data are presented in Table I.

These data show that the water content of Puget Sound medusae ranges from 96.5 to 97 per cent and is therefore similar to that previously found for other medusae (Hyman, 1938), although perhaps slightly higher. The salinity at Puget Sound was stated to be 3.09 per cent, hence slightly lower than that at Mt. Desert Island, Maine, where



Aurelia was found to have a water content of around 96.2 per cent. As previously pointed out (Hyman, 1938), the water content of medusae depends on the salinity of the sea water in which they are living, but unfortunately the salinity is often not stated in the literature. It is, of course, possible that hydroid medusae have a slightly higher water content than scyphomedusae but without concomitant data on the salinity of the sea water this cannot be decided.

The data in Table I suggest that young *Aequorea* have a slightly higher water content than grown ones. Statistical analysis shows that the difference in the water content of the small compared with the large *Aequorea* is significant, being 3.54 times its standard error.¹ It may therefore be concluded that the water content of medusae declines with increasing age (size) and this result is consistent with what is known of the water content of other animals. The data also indicate that the small species (*Phialidium*, *Sarsia*) have a slightly higher water content than the large ones (*Aequorea*, *Halistaura*) but the difference was found to be without sufficient statistical significance.

Dr. Earl Norris, of the chemical staff of the Oceanographic Laboratory, permits me to quote the following analysis of *Aequorea* made in his laboratory: water content, 96.45 per cent, salts (ash) 2.70 per cent, and organic matter 0.85 per cent. The salt content thus appears to be less than that of the surrounding sea water and indicates some degree of control by the animal of the passage of materials through its surface.

GENERAL BEHAVIOR

The behavior of these medusae was found to be correlated in many respects with their morphology. *Stomotoca* and *Sarsia* are Anthomedusae with a tall, narrow bell, and long pendent manubrium. *Aequorea*, *Halistaura*, and *Phialidium* are Leptomedusae, with a broad flat bell and a very short manubrium. The bell is relatively thin and flexible in *Phialidium* and *Halistaura*, so that it contorts with each pulsation, especially in the latter, but *Aequorea* has an unusual amount of jelly, rendering the bell stiff and inflexible, except at the margin.

Observed from the dock, all the species showed the same general behavior. All pulsate at an even rate for a period of time, then cease pulsations, float in any position for a while, then resume pulsations; and this alternation of activity and quiescence continues indefinitely. As is well known, the rate of pulsation is more rapid, the smaller the animal. The periods of pulsation and quiescence appeared to have no absolute

¹ The statistical calculation was kindly made for me by Mr. Daniel Lehrman, using Fisher's t-formula.

or relative time value² except in *Stomatoca*, which regularly pulsates 3-8 times in succession and then pauses for an interval equal to 1-4 pulsations. The degree of extension of the tentacles bears no relation to the bell activity, i.e., the tentacles might be contracted or fully extended in either pulsating or floating specimens. It has been reported for some medusae (i.e., *Gonionemus*, Yerkes and Ayer, 1903) that when they touch the surface, they turn over and float downward in an inverted position. No trace of any such behavior was seen in any of the five species listed. Touching the surface has absolutely no effect upon them.

Reactions to touch were tested by a blunt glass rod, mostly on medusae in the water reachable from the dock. The exumbrellar surface is in general highly insensitive and a light to moderate touch usually elicits no response. A tap or blow on the exumbrella results, in all the

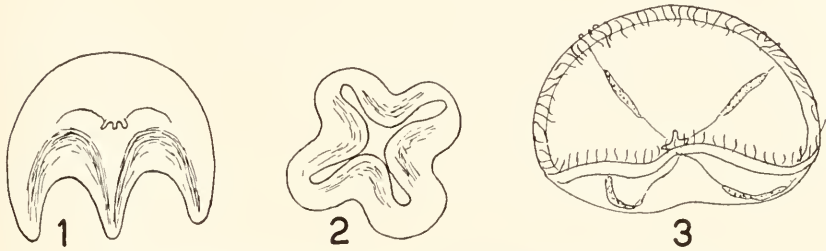


FIG. 1. Crumpling reaction of *Phialidium*, seen from the side.

FIG. 2. Crumpling reaction of *Phialidium*, seen from above.

FIG. 3. *Phialidium* giving the feeding reaction.

species except *Aequorea*, in a form of escape reaction which I call "crumpling."³ The animal ceases pulsations, folds in the bell to the smallest possible compass (Figs. 1, 2), and sinks. The very stiff bell of *Aequorea* is incapable of such a reaction and, in fact, *Aequorea* gives no response even to severe blows which knock it for several inches, except that it may miss a pulsation. Bumping into objects often evokes the crumpling reaction.

Mechanical stimulation of the bell margin, if effective, evokes either an escape reaction or the feeding reaction. The escape response may consist of the crumpling behavior noted above or of bell pulsations. The sensitivity of the margin appeared to vary with species. In *Hali-*

² Romanes (1885, p. 147) has recorded the number of pulsations and the duration of the rest periods in seconds for three specimens of *Sarsia* and also found no correlation between the lengths of active and quiescent periods.

³ What Romanes (1885, p. 123) called a "spasm" in *Staurophora*, "a sudden and violent contraction" causing the bell to assume a cuboidal form, is probably the same response as here termed "crumpling."

staura even a light touch often induced crumpling, whereas in the other species, a light touch was often ineffective. In *Phialidium* and *Sarsia*, marginal stimulation of the floating animal often resulted in the resumption of pulsations. *Stomotoca* and *Acquorea* were relatively insensitive to marginal stimulation. Strong marginal stimulation commonly results in crumpling in all forms except *Acquorea*. This animal, as already noted, is anatomically incapable of this type of escape reaction; to marginal stimulation, it either responds not at all or gives the feeding reaction, described below. Marginal stimulation may cause a cessation of swimming in a pulsating animal (*Phialidium*); this may be a form of feeding response. In the anthomedusan forms (*Sarsia*, *Stomotoca*), the manubrium, which hangs down below the level of the bell margin, appeared to be much more sensitive than the latter and would respond by crumpling or the feeding reaction to an intensity of touch which failed to evoke any response on the margin.

Response to light has been recorded for some medusae (*Gonionemus*, Morse, 1907; *Sarsia*, Romanes, 1885). In the forms here observed not the slightest response could be noted when they passed from a sunlit region into the shadow of the dock nor was any tendency ever seen to collect in either shaded or sunlit areas. The distribution of these medusae appeared to be determined wholly by the tidal currents and movements.

The water of Puget Sound near the laboratory is very cold, around 10° C. Any rise of more than a few degrees above this temperature diminishes the irritability of the medusae. At temperatures of 15–18° C., they tend to lie upon the bottom of the vessel in a flaccid, unresponsive condition, although pulsations continue. Weese and Townsend record that pulsations cease at 21–23° C.

Some medusae exhibit a food-catching ("fishing") behavior, swimming to the surface, then floating down, either right side up or inverted, with tentacles fully extended (*Gonionemus*, Yerkes and Ayer, 1903; *Limnocnida*, Edney, 1939). No food-catching behavior of any sort was witnessed in the Puget Sound medusae. They appear to depend wholly on chance contacts with suitable animals.

In the presence of food (giving off juices) *Gonionemus* shows excitement and makes random "searching" movements. The Puget Sound medusae, when placed in a vessel with a crushed bit of animal flesh, generally gave not the slightest sign of response even when quite close to the food. Occasionally, however, *Phialidium* when near the food would "hover" for a brief period. It seems probable that these medusae are capable of perceiving animal juice in the water.

THE FEEDING REACTION

To mechanical or chemical stimulation of the bell margin, all the species observed may give the feeding reaction. Mechanical stimulation consisted in touching the bell margin with a glass rod or forceps or moving the rod or forceps for a short distance along the margin. As already noted, such stimulation often evokes no response or may cause an escape reaction. Chemical stimulation consisted in touching a bit of animal flesh held in a forceps to the margin. As sources of food, fish, barnacles, *Mytilus*, crabs, etc., were used. The tentacles practically always grasp food and may grasp an inert object; the feeding reaction nearly always follows grasping of food by the tentacles, but does not invariably occur. If the feeding reaction fails to take place, the tentacles drop the food after a time.

The nature of the feeding reaction is correlated with the morphology of the animal. In the Leptomedusae (*Aequorea*, *Halistaura*, *Phialidium*) and also *Gonionemus* (Yerkes, 1902) with broad shallow bells, the reaction consists in the bending of the stimulated part of the margin to the manubrium (Fig. 3). The manubrium, which is very short in these forms, also moves to meet the inbent margin. The margin is held against the manubrium for a period during which the manubrium usually, but not invariably, grasps the food. When this has occurred, the margin returns to its normal position. If the manubrium fails to attach to the food, the margin will usually drop the food after a time. An *Aequorea* was observed in which the margin with food attached repeatedly bent to touch the manubrium until finally the manubrium grasped the food.

The following experiments were performed on *Phialidium*, which proved the most suitable form for studying the feeding reaction. If while one part of the margin is performing the feeding reaction, i.e., is being held against the manubrium, another part of the margin is stimulated, it too will give the reaction, providing the interval between the two stimulations is not too short. A third point of the margin may also be induced to respond; although stimulation of a third point may instead release another feeding reaction from the first region stimulated. The fact that the animals often fail to respond makes it difficult to study these reactions in detail or to investigate the question of fatigue.

The feeding reaction in the Anthomedusae (*Sarsia*, *Stomatoca*) differs from that of the Leptomedusae. These animals have a tall narrow bell and a long manubrium hanging below the level of the bell margin (Figs. 4, 5). The feeding reaction consists in the bending of the manubrium towards the stimulated part of the margin. The margin

does not show any movement. The manubrium was not seen to touch the margin but simply to make a nearly right-angled bend towards the stimulated region. In case of food held by the tentacles, the manubrial lip would touch and grasp the food.

In a leptomedusa which he called *Tiaropsis indicans* (stated by Mayer, 1910, to be probably *Eutimium socialis*), Romanes (1885) found that the tip of the manubrium would be precisely applied to any strongly stimulated spot of the bell. No such exact reactions were seen in any of the Puget Sound medusae.

In all the species observed, the lip of the manubrium (mouth frill) was found to be far more sensitive to chemical stimulation than any other part of the body. Food touched to the mouth frill was invariably

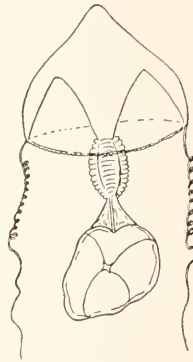


FIG. 4. *Stomotoca* with mouth frill attached to a *Phialidium*.

grasped. Probably the mouth frill in forms with a long manubrium is the chief agent in food capture.

Very few of the numerous medusae observed around the laboratory docks were seen to contain ingested food. It seems probable that the food requirements of these animals are low. *Sarsia* was never seen with ingested food. *Stomotoca* regularly attacks other medusae and was not infrequently seen with the expanded mouth attached to *Phialidium* (Fig. 4), sometimes to the larger forms. *Stomotoca* was also observed attempting to capture a crustacean larva, which escaped. *Phialidium* appeared to feed chiefly on small or minute plankters but might ingest larger crustacean larvae. *Acquorea* appeared to be a somewhat indiscriminate feeder and was observed with ingested crustaceans, *Nereis*, and peas and salmon refuse from adjacent canneries. Following a night run of a small *Nereis*, *Acquorea* and *Halistaura* would be seen on the next morning with ingested *Nereis*.

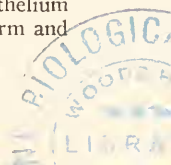
COURSE OF FOOD IN THE GASTROVASCULAR SYSTEM

As already mentioned, the chief purpose of these observations was to study the function of the gastrovascular system. To my knowledge, no proof exists that food is actually carried along the canals of this system, although statements to this effect are standard in textbooks. To study the matter, bits of fish, barnacles, *Mytilus*, or crabs were dipped into a thick paste made of powdered carmine and sea water and then touched to the mouth frill of medusae. Such bits were invariably grasped and usually, although not always, swallowed in a short time. *Stomatoca* and *Sarsia* proved rather refractory subjects and would often fail to ingest the piece of flesh. The course of the ingested material is easily followed by means of the red carmine.

Within half an hour after ingestion red material is seen spreading along the radial canals and within two or three hours it occupies the entire gastrovascular system. The material appears to be driven along the canals chiefly by the bell contractions. At each contraction, the material moves back and forth or swirls about. Gemmill (1919) in *Melicertidium* (correct name, *Melicertum*) found definite flagellar currents, running peripherally along the roof, centrally along the floor of the radial canals. Examination of Puget Sound medusae under the microscope failed to show any definite currents in the gastrovascular canals, although the flagella could be seen in active motion.

Immediately the food reaches any region of the gastrovascular system it is subject to ingestion by the gastrodermis,⁴ where it undergoes intracellular digestion. Surprisingly enough, however, the rôle of the gastrodermis in intracellular digestion varies greatly throughout the gastrovascular system. The chief sites of intracellular digestion are the gastrodermis of the manubrium and stomach (cavity at the upper end of the manubrium) and of the tentacular bulbs (basal swellings of the tentacles). These regions soon become stained deeply pink from ingested carmine particles (Figs. 5, 6, 7). Radial, circular, and tentacular canals take up some particles but play a minor rôle in comparison to manubrium, stomach, and tentacular bulbs. In forms such as the Leptomedusae which bear the gonads on the radial canals, those portions of the radial canals adjacent to gonad tissue were good sites of intracellular digestion; in non-gonadal regions the radial canals ingested very few carmine particles (Figs. 6, 7). In *Sarsia*, an expanded region near the manubrial tip is termed the stomach and is, in fact, the place where the ingested food is held, whereas in most medusae the stomach is an

⁴ I have elsewhere introduced the term *gastrodermis* for the inner epithelium of coelenterates, usually called entoderm, in the belief that the terms ectoderm and entoderm had best be restricted to embryonic stages.



expanded region in the summit of the bell, where the radial canals originate, and the food is passed into this chamber although, if too large, part of it remains in the lumen of the manubrium. In *Sarsia* it was found that the entire manubrium has as good digestive powers as the so-called stomach region (Fig. 5) and this was also the case with the other medusae. In short, the gastrodermis not only of the stomach but of the whole manubrium has high powers of intracellular digestion, equalled only by the gastrodermis of the tentacular bulbs. Sections through the tentacular bulbs of medusae showed that the gastrodermis is here highly columnar and packed with food vacuoles.

It is well known that in some hydroid medusae the radial canals open to the exterior by a pore near the bell margin (Fig. 7). These pores have been presumed to be excretory. In *Aequorea*, which possesses such pores, strands of mucus with entangled carmine particles were seen exuding from these pores a couple of hours after carmine feeding. This observation indicates that the pores may serve for the ejection of indigestible material.

Carmine particles persist in the gastrodermis for at least two or three days after feeding. The fed medusae were not retained long enough to determine the time interval required for complete elimination of the fed carmine.

GASTRIC JUICE OF AEQUOREA

Following the example of Beutler (1924), gastric juice was collected from *Aequorea* by feeding the animals small bits of sponge soaked in animal juice. Since it was soon learned that the juice of *Mytilus*, barnacles, etc., contains enzymes, all such juice was thereafter boiled. Small bits of boiled bath sponge were soaked in such boiled juice and then touched to the mouth frill of *Aequorea*, which always grasped them. Ingestion usually followed, but not infrequently the piece of sponge would be soon ejected. The experiments were not as satisfactory as hoped, because even when retained, the piece of sponge was seldom taken thoroughly into the gastric cavity, partly because of the incompressibility of the sponge and partly because of the stiff thick jelly of *Aequorea*. However, in many cases the sponges were retained in the manubrium for a considerable period. The pieces of sponge were then withdrawn with a forceps and their contained fluid expressed into a beaker. Some simple tests for enzymes were made with this fluid on litmus milk, bits of boiled animal flesh, and starch solution. The presence of a protease capable of dissolving animal flesh and of a lipase were indicated but anylase appeared to be absent.

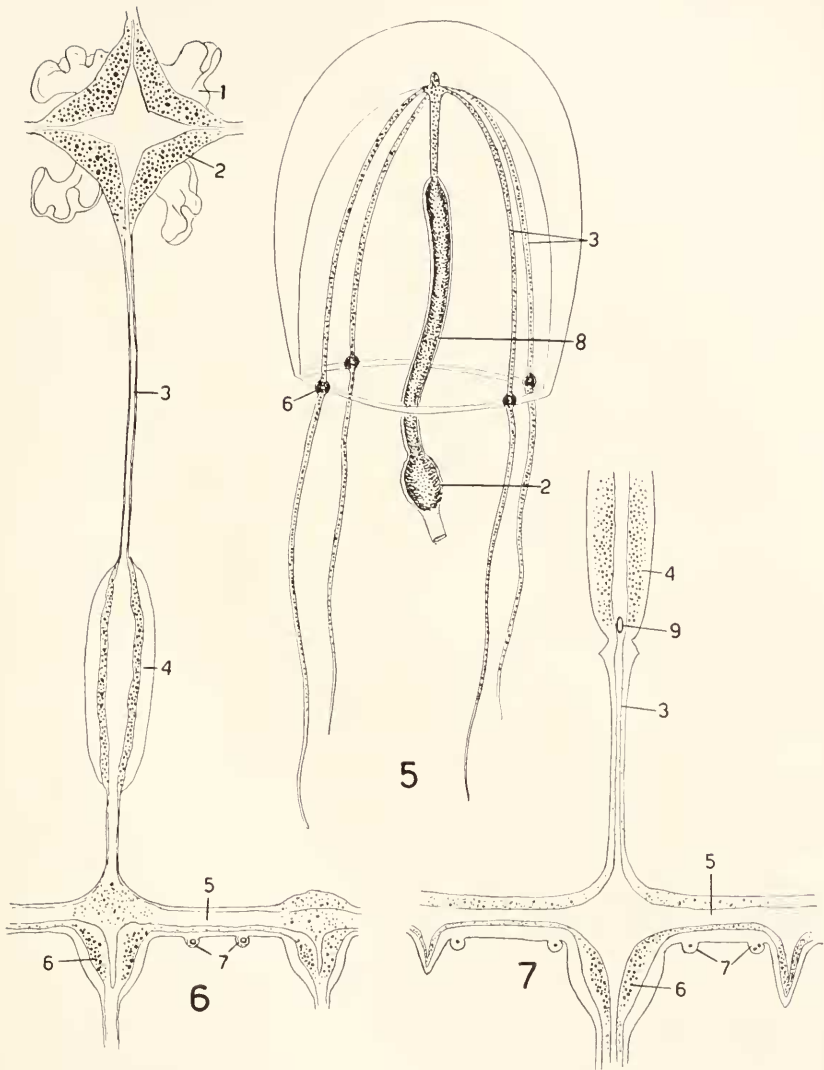


FIG. 5. *Sarsia*, following ingestion of carmine, showing distribution of carmine in the gastrodermis.

FIG. 6. *Phialidium*, stomach, one radial canal, and piece of margin, showing distribution of carmine in the gastrodermis, six hours after ingestion.

FIG. 7. *Aquorea*, piece of margin and adjacent part of one radial canal, showing distribution of carmine in the gastrodermis. Abbreviations: 1, mouth frill, 2, stomach, 3, radial canal, 4, gonadal region of radial canal, 5, circular canal, 6, tentacular bulb, 7, statocysts, 8, manubrium, 9, so-called excretory pore.

A number of *Acquorea* containing an ingested prey, chiefly *Nereis*, were captured and the gastric fluid removed by a fine pipette. Such fluid was in all cases but one more acid than the sea water, which has in Puget Sound a pH of 8.0–8.2. Of 12 individuals, the gastric juice was 7.2 in 1 case, 7.4–7.6 in 9 cases, 7.8 in 2 cases, and 8.0 in the twelfth specimen. A piece of *Mytilus* placed in the combined juice from four animals, with a pH of 7.4–7.6, was much dissolved in three hours, while a control piece in sea water was unaffected. The possibility, of course, remains that the acidity of the gastric juice might have come from the disintegrating prey.

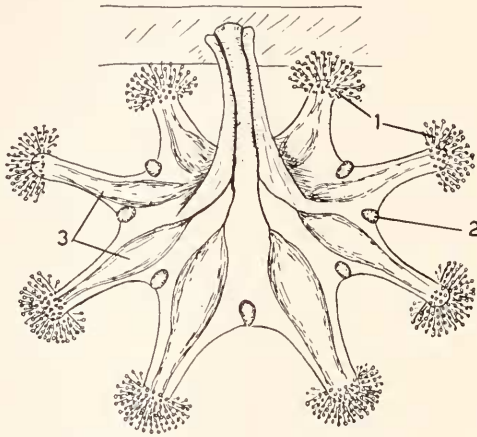


FIG. 8. *Haliclystus*, pendent from a seaweed, seen from the aboral surface, showing anchors and arms with tentacle clusters. 1, tentacle cluster, 2, anchor, 3, gonads.

BEHAVIOR OF HALICLYSTUS

The stalked scyphozoan, *Haliclystus sanjuanensis*, one of the Stauro-medusae, is common on seaweeds in a shallow bay of San Juan Island. During exceptionally low tides one can wade out and observe this interesting form in its natural surroundings.

Haliclystus (Fig. 8) has a trumpet-shaped body with the flaring oral end scalloped into eight arms, each terminating in a ball of small capitate tentacles. In the bottom of each scallop is an oval body, called the anchor, which, according to Schlater (1891), is provided with sensory cells and mucous glands. Seen in their natural habitat, the animals are fastened by the pedal disk to seaweeds and hang in a pendent attitude with the anchors erected. The medusa is relatively inactive. The chief activities seen in nature were: swinging on the stalk, flicking of the tentacles, sudden bending of an arm to the manubrium, or the folding

of all arms against the manubrium. When touched with a glass rod, the tentacle clusters might not react but often grasped the rod tenaciously and executed the feeding reaction. This consists of the quick bending of an arm so that the tentacle cluster touches the manubrium. It is very quickly given when food is touched to the tentacle cluster and arms other than the one touched may join in the reaction. The chief food in nature appeared to be the amphipod *Caprella*, common on the seaweeds where *Haliclystus* lives.

Brought into the laboratory, *Haliclystus* does not remain in good condition very long. Attempts to feed the animals with carmine-coated *Caprella* failed. The tentacles quickly grasped the food and bent with it to the manubrium which accepted it; but ingestion never ensued and the food was dropped after a time. Detached *Haliclystus* made strenuous efforts to reattach themselves, using the tentacle clusters for adhesion, but never succeeded even when placed on seaweeds. The tentacle clusters are extensively used in adhering to objects. No function could be discovered for the anchors. They were utterly unresponsive to mechanical or chemical stimulation, even severe pushing about, and although always credited with adhesive powers, were never seen to be employed by the animal for this purpose. The tentacle clusters appeared to be the most sensitive part of the animal. When touched they adhere and usually give the feeding reaction. Mechanical stimulation of the manubrium was ineffective; touching the subumbrellar surface usually evoked the feeding reaction in the adjacent arm. Strong mechanical disturbance of the animal may result in the infolding of all the arms, a response resembling the crumpling reaction of free medusae. Flicking of the tentacles or bending of the arms toward the manubrium were often witnessed without apparent cause; perhaps microscopic food is being caught at such times.

THE FUNCTION OF THE TENTACULAR BULBS OF HYDROMEDUSAE

The tentacle bases in hydroid medusae are commonly enlarged, forming the tentacular bulbs (Figs. 6, 7). The function of these bodies appears to have been frequently misunderstood. Because in some Anthomedusae each bulb bears an ocellus, the entire bulb is often called an ocellus in books and laboratory manuals. The bearing of an ocellus is, however, only one function of the tentacular bulbs and in fact not their usual function.

My study of the tentacular bulbs of a number of medusae has shown that the epidermis of these bulbs contains much sensory epithelium and is also a depot for the manufacture of nematocysts (these functions were already known). The epidermis is crowded with cnidoblasts in process

of secreting nematocysts and there can be no doubt that the tentacular bulbs furnish nematocysts for the rest of the body. I have also discovered, as already noted in the discussion of intracellular digestion, that the gastrodermis of the tentacular bulbs plays an important rôle in this process. This gastrodermis is a tall columnar epithelium which after food ingestion becomes packed with food vacuoles. The intense colors often seen in the tentacular bulbs and frequently carefully described in taxonomic accounts represent food materials in the gastrodermis of the bulbs and hence are of no systematic value.

In *Gonionemus* and other trachymedusae, the tentacular bulbs are often very large and conspicuous and partially or wholly detached from the tentacle bases. The tentacular bulbs of *Gonionemus murbachii*, found in the Eel Pond at Woods Hole, contain a black pigment and this has led to the erroneous idea that these bulbs are ocelli or "eye-spots." Thus in the last edition of Drew's "Invertebrate Zoology," it is stated that these bulbs are probably photosensitive, despite the fact that Murbach (1907) failed to find any evidence that they are more sensitive to light than other parts of the bell. I have not had any specimens of *G. murbachii* available for sectioning but I have sectioned the tentacular bulbs of *G. vertens*, the Puget Sound species, fixed in Flemming's fluid for the purpose. The sections show no trace of a photoreceptor in the bulbs of this species although there is an abundance of sensory epithelium. In fact, photoreceptors are not known to occur in any of the Olindiidae, the family to which *Gonionemus* belongs. I think it may safely be concluded that the species of *Gonionemus* are devoid of special photoreceptors although these medusae do react to light.

The tentacular bulbs of hydromedusae thus have three important functions: they act as depots for the manufacture and storage of nematocysts, they are organs of general sensory perception, and they are very active in intracellular digestion.

SUMMARY

1. Studies were made in Puget Sound on several medusae belonging to the groups Anthomedusae (*Stomotoca*, *Sarsia*), Leptomedusae (*Aequorea*, *Halistaura*, *Phialidium*), and Stauromedusae (*Halicyllistus*).

2. The water content was determined for four species (*Aequorea*, *Halistaura*, *Phialidium*, *Sarsia*) and found to range from 96.5 to 97 per cent (salinity of the sea water 3.09 per cent). Evidence was obtained that the water content declines slightly with increasing size.

3. Activities are limited and responses cannot be elicited with dependable regularity.

4. All species observed have alternate periods of pulsation and floating; in general these periods bear no absolute or relative time duration to each other.

5. Behavior is correlated with morphology and hence shows characteristic differences between the different groups.

6. Mechanical or chemical stimulation, when effective, elicits either an escape reaction or the feeding reaction.

7. The escape reaction may consist of bell pulsations but to stronger stimuli a general contraction, termed crumpling, accompanied by cessation of swimming, is given. *Aequorea* is anatomically incapable of this escape reaction because of its thick stiff bell.

8. The feeding reaction consists in the Leptomedusae and *Haliclystus* of bending the stimulated region of the margin to the manubrium which also moves to meet the inbent margin. In the Anthomedusae it consists of turning the long manubrium in the direction of stimulation.

9. Food was traced through the gastrovascular system by feeding bits of animal flesh coated with carmine. Within half an hour after feeding, food begins to spread along the radial canals and in two or three hours occupies the entire gastrovascular system.

10. The principal sites of intracellular digestion are the lining epithelium of the manubrium, stomach, and tentacular bulbs. Radial, circular, and tentacular canals play a minor rôle. Those portions of the radial canals adjacent to gonads (Leptomedusae) are much more active in intracellular digestion than radial canals elsewhere.

11. No definitely directed flagellar currents could be observed in the gastrovascular system.

12. Strands of carmine-containing mucus were seen to be extruded from the so-called excretory pores of the radial canals (*Aequorea*).

13. The fluid from the stomach of *Aequorea* is usually considerably more acid than sea water (to pH 7.2, mostly 7.4–7.6). It contains a proteolytic and a lipolytic enzyme but appeared to be devoid of diastases.

14. Feeding and escape reactions of *Haliclystus* (a sessile stauromedusan) are similar to those of Leptomedusae. No function could be found for the anchors; the animal gave no response to chemical or mechanical stimulation of the anchors nor were they used for adhesion.

15. The tentacular bulbs of hydromedusae function as depots for the manufacture and storage of nematocysts, as organs of general sensory perception, and as important sites of intracellular digestion. They are not photoreceptors although in Anthomedusae they bear the ocelli when these are present. The tentacular bulbs of *Gonionemus* are devoid of differentiated photoreceptors.

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